be used to assess if that proportion of the variance in TMW unrelated to body size is related to ToB. Although smaller kingbirds may nest earlier than larger ones ($P = 0.06$ is certainly suggestive of that), Murphy's conclusions referring to "a direct energetic basis for differences in ToB" (p. 468) were premature.

Third, removing an outlying point in bivariate plots is invalid unless there is good reason to suspect that the observation came from a bird that was not part of the *statistical* population being studied, e.g. a non-breeder instead of a breeder, a yearling instead of an adult, etc. Murphy argued that one female "laid unusually early" and used this as justification to ignore her, thereby resulting "in a highly significant relationship" (his fig. 2). Murphy stated further that the patterns in fig. 4 were obscured by one "nest in particular" that "eliminated several potentially significant relationships"; no reason was provided for discarding that observation. We note, however, that Murphy did not ignore the equally "unusual" female (in fig. 2) that nested late, at about the 66th day, with about 4.5 g of TMW. We suggest, from inspection of fig. 2, that had Murphy discarded the "unusually" late female instead of the unusually early one, his analysis would have shown a negative relation between TMW and ToB! Equally invalid reasoning could be used to justify ignoring the female in fig. 2 that produced 4 eggs but was "unusual" in that she had a much higher TMW than any other female that laid 4 eggs. Outliers are most influential when sample sizes are very small, and thus *a posteriori* decisions to remove them must be well justified. If such justification is not evident, then formal procedures for objectively detecting outliers should be used (e.g. Sokal and Rohlf 1981: 413, Owen and Chmielewski 1985). Regardless, robust inferences generally are precluded if small sample sizes are used for statistical analyses.

We do not believe that Murphy, given the timing of collections and the number of birds analyzed, could have tested his hypotheses about timing of breeding, clutch size, and egg composition of Eastern Kingbirds. We view those sections of the paper that deal with the relation between body size and ToB as exercises in data exploration—a procedure that is useful for formulating hypotheses. Murphy has shown that smaller female kingbirds may nest earlier than larger ones, but clearly other data are required to investigate why they do.

We thank D. M. Scott and T. W. Arnold for their comments on this manuscript.

LITERATURE CITED

ANKNEY, C. D., & C. D. MacINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95: 459–471.

——, & D. M. SCOTT. 1980. Changes in nutrient reserves and diet of breeding Brown-headed Cowbirds. Auk 97: 684–696.

BLEM, C. R., & J. F. PAGELS. 1984. Mid-winter lipid reserves of the Golden-crowned Kinglet. Condor 86: 491–492.

HAILS, C. J., & A. K. TURNER. 1985. The role of fat and protein during breeding in the White-bellied Swiftlet (*Collocalia esculenta*). J. Zool. London 206: 469–484.

JONES, P. J., & P. WARD. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea *Quelea quelea*. Ibis 118: 547–574.

MURPHY, M. T. 1986. Body size and condition, timing of breeding, and aspects of egg production in Eastern Kingbirds. Auk 103: 465–476.

OWEN, J. G., & M. A. CHMIELEWSKI. 1985. On canonical variates analysis and the construction of confidence ellipses in systematic studies. Syst. Zool. 34: 366–374.

SOKAL, R. R., & F. J. ROHLF. 1981. Biometry. San Francisco, W. H. Freeman and Co.

Response to Alisauskas, Ankney, and Krementz

MICHAEL T. MURPHY[1]

Alisauskas et al. (1987) claimed that my recent analysis of body composition in Eastern Kingbirds (*Tyrannus tyrannus*; Murphy 1986a), and the relation of composition to reproduction, was flawed. Further, they charged that my conclusions concerning the relation

[1] Department of Life Sciences, Indiana State University, Terre Haute, Indiana 47809 USA.

between female body composition and egg composition were "derived illogically." I here provide body composition data for prelaying females, and defend my measures of size and conclusions concerning the determinants of egg composition. I also discuss my rationale for deleting points in particular analyses.

First, I collected and analyzed the body composition of 5 prelaying female kingbirds. I did not report the data (except for bone weights; see table 5) because

I could not claim unequivocally that they were residents since I could not associate them with nests (migration was still underway). Assuming they were residents, then mean total muscle weight (TMW) for prelaying females and for females that laid either 2 or 3 vs. 4 eggs were 4.23 g, 4.38 g, and 4.18 g, respectively (analysis of variance, $F = 0.76$, df = 2,24, $P = 0.48$). Mean standard flight muscle weights (SFMW) were analyzed similarly with identical results: 3.00 g/mm^3, 3.06 g/mm^3, and 2.80 g/mm^3 (all $\times 10^{-6}$; $F = 0.74$, df = 2,24). The single female collected during egg laying had a TMW of 4.17 g and a SFMW of 3.00 g/mm^3. Although a larger sample would have been preferable, there is no suggestion of a change in muscle weights over the laying cycle. Alisauskas et al.'s fears that I failed to record a buildup of reserves for clutch formation are thus unfounded, but I thank them for providing the opportunity to clarify my analysis (but see my comments on p. 471).

However, Alisauskas et al. failed to mention that my conclusion that nutrient or energy availability did not limit clutch size was influenced substantially by the comparison of egg and body composition (p. 474). Alisauskas et al. thus provided only half the story. I stand by my conclusion that clutch size in kingbirds was not limited by nutrient availability, and that energy and nutrients for egg formation come mainly from immediate dietary sources (e.g. Ankney and Scott 1980).

Alisauskas et al. objected greatly to my use of TMW as an estimate of body size and claimed I "confused body size with body condition." They argued that factor 1 scores from a principal components analysis of skeletal elements provide an unbiased and the *best* estimator of overall size. I performed the PC analysis, and compared body size with timing of breeding (ToB) using factor 1 scores, TMW, and flight muscle weight (FMW). The authors' accusation that "Murphy altered his definition of size" when the correlation between factor 1 scores and ToB were found to be only marginally significant is unfounded. The data analysis section of the Methods (p. 467) clearly stated that "Measures of body size included FMW, TMW, and linear morphological measurements of size." As it turned out, ToB correlated most strongly with TMW ($r = 0.507$, $P = 0.014$), indicating that females with the smallest muscle weights bred first, which I believe was a function of their lower overall energy maintenance costs compared with larger females. (The correlation coefficient quoted by Alisauskas et al., $r = 0.58$, is wrong. The latter value pertains to the reduced sample of females that laid 2- or 3-egg clutches, not the entire sample. See fig. 3.)

Alisauskas et al.'s objection to my use of TMW assumed that muscle weight changes rapidly over short time periods and that it actually reflects condition and not size. They purported to provide an example of short-term changes in body condition (Blem and Pagels 1984) that is, first, inappropriate and, second, incorrectly used to support their position. Blem and Pagels examined diel variation in body composition in Golden-crowned Kinglets (*Regulus satrapa*) in Ohio during midwinter. Comparing one of the smallest (8 g) North American passerines in midwinter to the Eastern Kingbird (40 g) during the breeding season in Kansas is suspect, at best. Blem and Pagels found that the lean, dry muscle weights of kinglets did *not* vary over short time periods, but lipid levels did. My measure of TMW was free of fat and water. Given that TMW in kingbirds did not differ between prelaying females, and postlaying females that produced different numbers of eggs, I maintain that TMW does not vary substantially over short time periods during the breeding season in kingbirds. Moreover, I argue strongly that TMW is the single best estimate of size when testing questions dealing with the energetic consequences of body size. Alisauskas et al.'s reliance on factor 1 scores to estimate size is wrong from an energetics standpoint. A long-boned individual would appear as a large bird in a principal components analysis even if it had a small TMW and was thus very "thin." Without information on TMW, factor 1 scores provide a reasonable estimate of size. PC analyses are not a panacea, however, and one's measure of size may vary with the question being asked.

Alisauskas et al. have a legitimate complaint with my decision to delete the large, early-breeding female with a 3-egg clutch from the comparison of ToB with TMW for females laying 2 or 3 eggs (see fig. 2). The inclusion of this female reduced the correlation from 0.580 ($P = 0.01$) to 0.386 ($P = 0.12$) in this subsample of birds. However, their claim that a negative relationship would have occurred if instead I had deleted the late-breeding female on day 66 is an exaggeration ($r = 0.140$). I note also that the authors failed to mention the significant relationship between ToB and TMW in females with 4 eggs ($r = 0.870$, $P = 0.03$), or that when I took the conservative approach and treated all females equally (this was my initial analysis, p. 468), ToB correlated with TMW ($r = 0.507$, $P = 0.014$).

I suspect that part of the reason for our disagreement about the biological significance of the correlation between egg weight and SFMW in kingbirds (fig. 3, $r = 0.463$, $P = 0.03$) lies in my use of the term "condition." SFMW did not vary between pre- and postbreeders, and is actually a measure of the relative size of the flight musculature. It is not an estimate of condition in the sense of providing nutrients directly for reproduction. Given that SFMW did not vary over the laying period, I hold that it accurately reflected starting conditions. Hence, Alisauskas et al.'s statement that my conclusions concerning egg size were "derived illogically because body condition of postlaying females cannot affect the sizes of eggs that already have been laid" does not apply. A *portion* of egg-size variability was related to the *relative* size of the flight muscles. I hypothesized that this was be-

cause the pectoral muscles were used for short-term (i.e. daily) storage of lipids used in egg formation. Large eggs also required more minerals for shell formation, and this was presumably the basis for the negative relation between egg size and body minerals. I fail to see why opposite signs in these slopes caused problems for Alisauskas et al.

Lastly, Alisauskas et al. objected strongly to my treatment of the egg composition/female body composition data because I chose to exclude one point from the analysis because it "eliminated several potentially significant relationships" (see fig. 4). My rationale for excluding this point was simple: given the virtual nonexistence of this type of data (but see Houston et al. 1983), I felt it would be reasonable to *speculate* as to the basis for differences in egg composition among females. I make no apologies for this. Healthy speculation, which I consider the egg composition/body composition data to be, is required for generating and testing new hypotheses.

The data on kingbirds provide one of the strongest supporting cases for Downhower's (1976) body-size/timing-of-breeding hypothesis. Relative to the other years of my study, timing of breeding was delayed in the year in which these data were collected (Murphy 1986b), and it is probable that one is most likely to detect body size-dependent breeding under such conditions. In years of more benign conditions body size may have little effect on breeding date. Nonetheless, intermittent selective events such as this can be ecologically and evolutionarily important (e.g. Johnston and Fleischer 1981). If Alisauskas et al. still object, it is their responsibility to provide a more co-gent explanation for the observed direct relationship between body size and timing of breeding in kingbirds.

LITERATURE CITED

ALISAUSKAS, R. T., C. D. ANKNEY, & D. G. KREMENTZ. 1987. Body condition in Eastern Kingbirds. Auk 104: 546–547.

ANKNEY, C. D., & D. M. SCOTT. 1980. Changes in nutrient reserves and diet of breeding Brownheaded Cowbirds. Auk 97: 684–696.

BLEM, C. R., & J. F. PAGELS. 1984. Mid-winter lipid reserves of the Golden-crowned Kinglet. Condor 86: 491–492.

DOWNHOWER, J. F. 1976. Darwin's finches and the evolution of sexual dimorphism in body size. Nature 263: 558–563.

HOUSTON, D. C., P. J. JONES, & R. M. SIBLY. 1983. The effect of female body condition on egg laying in Lesser Black-backed Gulls *Larus fuscus*. J. Zool. London 200: 509–520.

JOHNSTON, R. F., & R. C. FLEISCHER. 1981. Overwinter mortality and sexual size dimorphism in House Sparrows. Auk 98: 503–511.

MURPHY, M. T. 1986a. Body size and condition, timing of breeding, and aspects of egg production in Eastern Kingbirds. Auk 103: 465–476.

———. 1986b. Temporal components of reproductive variability in Eastern Kingbirds (*Tyrannus tyrannus*). Ecology 67: 1483–1492.

Female Choice in Middendorff's Grasshopper-Warbler?

JILL P. LIGHTBODY[1]

Recently, Nagata (1986) suggested that the polygyny-threshold (Verner 1964, Verner and Willson 1966, Orians 1969) and sexy-son (Weatherhead and Robertson 1977, 1979) hypotheses may be applicable models for female choice in monogamous species. He suggested also that female Middendorff's Grasshopper-Warblers (*Locustella ochotensis*) base their choice of mate on the quality of the male's territory rather than of the male.

The polygyny-threshold and sexy-son hypotheses were developed to explain why some males in polygynous species acquire more than one mate while others have only one. These hypotheses are useful as tools to understanding female choice only in polygynous species, not in monogamous species. To imply that the polygyny-threshold hypothesis is synonymous with a hypothesis that holds that females base their choice of mate on the quality of his territory is misleading. Under this hypothesis, females are assumed to assess the quality of the breeding situation, which includes the quality of the male. To imply that the sexy-son hypothesis is synonymous with the hypothesis that females choose mates based on the quality of the male alone is also misleading. Again, under this hypothesis, females are assumed to base their choice of mate on the quality of the territory as well as the male. The two hypotheses differ in the way females should be compensated for choosing a polygynous situation over a monogamous one. The polygyny-threshold hypothesis suggests that females

[1] Department of Biology, Mount Allison University, Sackville, New Brunswick E0A 3C0, Canada.